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Distribution and Movements of Desert Plants.

By VOLNEY M. SPALDING. Carnegie Institution of Washington, Publication No. 113, issued October 22, 1909.

Those who have for some years expected the publication of Professor Spalding's arduous and prolonged studies of the desert vegetation of the southwest, but more particularly in the vicinity of the Desert Botanical Laboratory, welcome it in a peculiar sense of gratification. The work, entitled as indicated above, embraces, to be sure, a wider range of observation than that within the purview of the leading author. The following are the themes discussed: Plant Association and Habitats; Local Distribution of Species, in which Cannon's studies on root distribution are made use of; The Lichens, by Professor Bruce Fink; Environmental and Historical Factors, including the geology and soils of the vicinity of the Laboratory Domain, by Professor C. F. Tolman and Professor B. E. Livingston, respectively; The Vegetative Groups, by Professor J. J. Thornber; The Origin of Desert Flora, by Dr. D. T. MacDougal; followed by a general discussion. This serious attempt to correlate the results of specialists in a vegetational study has everything to commend it, and the results which have emerged fully justify the expectation that this method of procedure will, for the future, serve an increasingly important rôle.

Aside from the hydrophytes, of minor interest in the work before us, the range of biological types found in the Tucson region includes two ecological groups, the xerophytes, generally distributed on the slopes and "mesas" so called, and the mesophytes, which are found especially near the watercourses and, as the result of irrigation, in the flood plains. This distinction in habitat is, however, operative only in general. The shade afforded by other plants and the nooks of sheltering rocks extend, very locally, into the drought period, the mesophytic conditions established by a rainy season. It thus comes about that antithetically pronounced mesophytes and xerophytes frequently stand close together in contingent habitats. It is to be

noted, however, that the mesophytic conditions are relative and may not be compared with their analogues in the eastern or northern United States.

The winter and summer rains produce two mesophytic seasons of varying length, according to the character of the precipitation. These are times of rich vegetation of annuals, which, however, are not common to the two seasons. Thornber, by experiment, has shown that the temperature relations exhibited by the seeds of these annuals are prepotent in fixing their times of germination.

It is noted that the cryptogamic elements of the vegetation are relatively unimportant. The reviewer has had occasion to remark the very striking difference in this regard between the desert about Tucson, and that of north Zacatecas, where the land cryptogams, including algæ, lichens, bryophytes and pteridophytes are much more in evidence. This difference may be charged to a lower rate of evaporation in Zacatecas, as also may the general as well as local differences in the occurrence of phanerogamic as well as cryptogamic parasites. These, in the Tucson desert, are very inconspicuous; the cases noted by Spalding are *Phoradendron* on the mesquite and a root parasite *Orthocarpus*, studied by Cannon.

The mesquite is recognized as the dominant element in the mesquite forest association of the flood plain. While adapted to low degrees of atmospheric humidity, its demands for soil water are relatively high. Its maximum development is therefore in the flood plain, in which situation its roots are in correspondence with "a sufficient water supply." Its success in maintaining its foothold is attributed to the effective root system "always within reach of a permanent, deep water-supply." The reviewer takes this not of necessity to mean a water table. At any rate, it is certainly known that vast mesquite areas are to be found where no water table has been discoverable within several hundreds of feet. The high capillarity of the very fine, compact, very deep soil of the flood plain is sufficient to explain the presence of the mesquite.

The mesquite occurs also along washes, but

is of smaller size, and still smaller is it when present on the hillsides. The distribution, as indicated by its size, is evidently indicative of the different amounts of available soil moisture. The reviewer has noted that large mesquite occurs on hillsides in Zacatecas, where there are hidden springs, as indicated by an actual outflow some distance away.

The mesquite in respect to water-supply is a physiological type to which belong, *e. g.*, *Koeberlinia spinosa*, *Holacanthus* sp. The water relations of these plants have given rise to a saying in Mexico: *Donde hay junco, hay agua*, "where the junco occurs, there also is water," upon which faith many a dry well has been dug. This *à propos* of the occurrence of mesquite in the flood plain.

Of the more distinctly desert associations is Spalding's creosote-bush (*Larrea*) association. This is almost coincident with the mesa-like slopes of low gradient so characteristic of desert regions. Untoward physical conditions are here—a soil with little capacity for water retention, and underlaid by an impervious hardpan of caliche. To the most rigorous of these conditions the creosote-bush is the last to succumb, and is often the only plant with a perennial foothold.

The peculiarities of local distribution contingent upon the aspect of slopes, especially the steeper ones, have been extremely well studied by Professor Spalding, and the maps, made in detail and accuracy hitherto unequaled, by Mr. J. C. Blumer, to record observations, rather than merely to illustrate the principles involved, are in themselves a noteworthy contribution. Five species have been thus studied in detail. Of these, the most compelling example, by virtue of its size and appearance, is the sahuaro, *Cereus* (now *Carnegiea*) *giganteus*. This principally affects the southern aspects of the hills, the "optimum physical habitat" for this plant. The author has endeavored in this, as in the other cases treated, to refer this peculiar distribution to an efficient cause or set of causes. The search for these has led Professor Spalding to very important conclusions. Thus, the choice of habitat is, in many cases, condi-

tioned by "difference in habit, and power of accommodation," leading to a fixation in particular situations. On the other hand, some plants are distinguished by a wide capacity for adjustment, and hence the restrictions upon choice of habitat are less strait and insistent. Here is pointed out that physiological adjustment may be of far more importance than structural "adaptation," but it appears—and this is of major importance—that in both cases "inherited peculiarities determine the limits of choice." Apparently the evidence does not indicate a progressive (racial) change in adaptation, but that a chance pre-fitness determines the possibilities of getting along.

Of chief importance appears to be the "range of temperature, though other factors, in certain cases at least, are involved." A constructive criticism at this point may be made that temperatures may be of this degree of importance in only a secondary way, but this also in certain cases. The view seems justified that the differences of insolation, and so of the temperatures, on slopes of opposite aspect, is effective in selection as between plants, which, during germination, quickly attain a sufficient (and again inherited) degree of structural or physiological resistance and those which are slow in this regard. The conclusions before us strongly indicate the great importance of the study of seedling development, and it may be believed that much light will thus be thrown on many still obscure questions of distribution.

Nevertheless, Professor Spalding makes a strong case for the direct effect of temperature, as *e. g.*, in the case of the sahuaro, whose limits of distribution appear to be set by temperature limits. It would be of the greatest interest and profit to compare, for this plant, its temperature environment, *e. g.*, in the Sta. Catalina Mountains and those of its present, generally northern, geographical range.

The so well-known individual isolation of desert plants has given force to the idea very generally accepted, that their interrelations are of minor importance. Pause is given to

this view, and while no detailed study is as yet available, it is pointed out that *vigorous competition is the rule and not the exception*. The "mutual accommodation" of certain plants as seen in the non-interference of the root systems (Cannon) is referred to; thus, the proximity of certain species involves the minimum of competition. Accommodation appears to the reviewer, therefore, as to Dr. Cannon, to be a minor degree of competition, or at least involves at some time a struggle. It frequently happens, *e. g.*, that the sheltering protection of an established plant results only in establishing active competition, frequently of minor but often of greater vigor, between it and its protégé. In this connection is of interest an account by Dr. Cannon, of the root system of *Cereus (Carnegiea) giganteus* and its mutual relations with those of three other species, discovering important topographic differences, which result that the roots of these plants, growing close together, are rarely in physical contact, because, chiefly, they do not occupy the same soil horizon, though "this does not mean that the plant (*Cereus*) is free from competition." It is further developed that the cacti are chiefly characterized by a relatively much more important lateral, shallow root system, and sees in this an important adjustment for aeration, in the absence of foliage, as well as to mechanical support, and for the remarkable readiness with which slight precipitation is made use of.

Professor C. F. Tolman gives an account of the geology of the vicinity of the Tumamoc Hills, where stands the laboratory. Two matters of more general interest emerge, namely, the origin of the wide slopes of gentle gradient, above referred to, and that of the "caliche," the calcareous hard-pan which plays an important rôle in its relation to the vegetation. Professor Tolman contends for the sub-aerial deposition of the clinopains (Herrick) or conopains (Ogalvie) and applies to these the simple, but unfortunately generic name of "slopes," to which the reviewer had previously applied the more specific term, foot-slope. To him—perhaps for human reasons alone—the latter appears the more descriptive and ap-

propriate name. But we are more interested in Professor Tolman's views—concerning the materials composing the slopes. They are derived from the steeper mountain slopes above, which are, under semi-arid conditions, strongly attacked by torrential precipitation. The slope is, as said, of sub-aerial origin, in the formation of which temperature change and gravity play the leading parts, running water bearing "a varying rôle." This view is asserted chiefly for the reason that it controverts an earlier interpretation which calls upon a former marine or lacustrine extension to explain the topographical uniformity of the foot-slopes. Professor Tolman says that "deposition" in the playa is "most active during periods of water occupancy, when the dust from the mountains and slopes is caught by the water sheet." The evaluation of the factors at work is, however, confessedly difficult, but the reviewer suggests that, in undrained playas, the moving water sheet on the lower zones of the foot-slopes and the arroyo-imprisoned streams of their upper zones, consequent on heavy precipitation, are of great importance in eroding and carrying finer detritus to be laid down by the standing water sheet. As a matter of observation, this seems to be an important condition at the present day in certain regions.

The explanation of the caliche—this, Professor Blake's name, is retained—accords, with slight modification, with that of Professor Forbes. Caliche is, according to the latter, a "mixture of colloidal clay and carbonate (mainly) of lime," carried by the rain water downward into the soil to the depth, a few inches to three or four feet, where, as the result of desiccation, the hard-pan is formed. Professor Tolman finds, however, a ready supply of calcareous matter, coupled with an absence of drainage to remove it, to favor the encrustation. The rapidity with which caliche may be formed under experimental conditions out-of-doors may be remarkable—two inches in two years. The body of Professor Tolman's paper treats of the topography, geology and petrography (based on the work of Professor F. W. Guild) of the laboratory domain. This

part the reviewer leaves to a more capable pen. Professor B. E. Livingston contributes a section on the soils of this domain. He describes these soils in some detail, and there follow data derived from a detailed study of the soil moisture content at given depths for a period extended between October 3, 1907, and April 11, 1908. The importance of such information is shown in the fact that the effect of precipitation lags behind the precipitation itself, which "consideration emphasizes the inadequacy of mere precipitation data in any attempt to determine the moisture conditions under which the plants of any region live." Elsewhere, Professor Livingston points out that the "distribution of plant forms is perhaps more often determined by availability of oxygen than that of water," and this is of importance for desert plants, many of which appear to suffer from lack of oxygen in soils too abundantly supplied with moisture. Professor Spalding concludes that the facts established by Livingston show a remarkable degree of correspondence with the facts of distribution.

Professor J. J. Thornber, in a few pages, gives an exceedingly important summary of the vegetation groups of the domain. The unimportance of biennials is remarked, only three species being noted, in contrast to a total of 230 annuals. Of these, the winter annuals are three times more numerous than those of the summer. The total number of perennials is about equal to that of the annuals. Numerically the grasses (70 sp.) and the compositae (65 sp.) are dominant.

Of the lichens, of which at any rate 24 species are reported, enough, based on the study of them by Professor Bruce Fink, is said to indicate that a fruitful field of study awaits one who is disposed to attack these organisms in their desert habitat from an ecological point of view.

Dr. D. T. MacDougal deals trenchantly with the live question of the origin of desert plants. He sees little evidence that individual capacity in the soma has resulted in adaptation to desert conditions. The mesophytic forms which have extended to the desert

regions flourish only during the mesophytic periods. Observed responses to true desert conditions are not necessarily adaptive, nor is it possible to refer highly specialized characters to the "supposedly causal conditions which they meet," such as the spines and glochidia of cacti. This is well said.

The weight of experimental evidence, derived from the work of Tower, Gager and MacDougal, the latter especially, indicates that the effects of environmental changes in the germ plasm are accountable for "irreversible changes in a hereditary line by which new combinations of qualities and new characters" become "fully transmissible." Dr. MacDougal properly points out the mental bias which has led to the regarding of desert plants as highly specialized, and mesophytes as not. What would the trained botanist of desert antecedents have thought on viewing, for the first time, a mesophytic forest!

It is clear from this cursory glance at the volume under review, embracing only a few of its more striking features, that a great deal of careful, insistent inquiry has been carried on by all the authors. This, it is equally evident, is leading us steadily in the direction of illuminating generalizations, which express more rational notions about plants than those which have held the botanical mind in thrall for many years. We are getting, as an example, a proper notion of adaptation, by which the word itself is condemned. This notion is not new, but is widely unaccepted in practise as yet, and this is well enough if it forces us to bring about an adequate investigation of the facts.

Much remains to do, or, better, shall we say truth if we admit that even the beginnings yet made are small. But beginnings in the right direction are notable, and Professor Spalding's work is such. The reviewer avows his warm admiration and regard for him who, after many years of rare service as a teacher, has devoted much of his remaining strength to a trying field of research, fruitful of basic truth in method and result.

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